MYCOTAXON

ISSN (print) 0093-4666 (online) 2154-8889 Mycotaxon, Ltd. ©2021

April–June 2021—Volume 136, pp. 497–509
https://doi.org/10.5248/136.497

Chlorophyllum hortense newly recorded, and *C. molybdites* confirmed, from Pakistan

Sana Jabeen[1*], Shahzeena Arshad[1], Humaira Bashir[2],
Mughees Hamid[1], Aneela Yasmeen[3], Abdul Nasir Khalid[2]

[1] *Department of Botany, Division of Science & Technology, University of Education, Township, Lahore, Pakistan*
[2] *Institute of Botany, University of the Punjab, Quaid-e-Azam Campus-54590, Lahore, Pakistan*
[3] *Centre of Excellence in Molecular Biology, University of the Punjab, Lahore, Pakistan*
* Correspondence to: *sanajabeenue@gmail.com; sanajabeen@ue.edu.pk*

Abstract—During a field survey of macrofungi from Kasur and Narowal districts, Punjab, Pakistan, some collections were found morphologically similar to species of *Chlorophyllum*. Their morphological and molecular analyses revealed two species, *Chlorophyllum hortense* (a new record from Pakistan) and *C. molybdites* (confirming a previous Pakistani record that lacked phylogenetic and detailed micro-morphological analyses).

Key words—*Agaricaceae*, agaricoid, ITS, taxonomy

Introduction

Chlorophyllum Massee is a relatively small genus in the *Agaricaceae* (Vellinga 2004b, Vellinga & al. 2011, Ge & Yang 2006). Species within this genus are saprobic, distributed in tropical to temperate regions of the world, and often found growing in urban and rural habitats (Vellinga 2004a). The genus varies from agaricoid, secotioid to gasteroid in habit. Agaricoid species are characterized by a hymenodermal pileus covering, smooth stipe, and basidiospores that either lack a germ pore or have a germ pore caused by a depression in the episporium without a hyaline covering, and a white, green, brownish or brown spore print (Vellinga 2003a, 2004b; Vellinga & al. 2011, Ge & Yang 2006, Crous & al. 2015, Loizides & al. 2020).

Chlorophyllum was previously recorded from Pakistan by Razaq & Shahzad (2012), who provided descriptions and illustrations of *C. molybdites* and *C. rhacodes* [as *Macrolepiota rachodes*], but without phylogenetic analyses and more detailed descriptions these cannot be accepted as authenticated identifications. Our research focuses on the identification of *Chlorophyllum* specimens collected in Kasur and Narowal districts of Punjab, Pakistan. The identification of taxa is based on both morphological characters and nrDNA ITS phylogenetic sequence analysis.

Material & methods

The samples were collected from Kasur and Narowal district, Punjab, Pakistan during monsoon of 2015 and 2019.

The Köppen–Geiger climate classification (Geiger 1954, 1961) describes the climate of Kasur district as warm semi-arid. Ground vegetation was sparse at the collection site, with patches of grass along the bank of BRB canal. Dominant tree species include *Dalbergia sissoo* DC. and *Vachellia nilotica* (L.) P.J.H. Hurter & Mabb. Köppen–Geiger (Geiger 1954, 1961) classifies the Narowal district as humid subtropical. The collection site was a grassy ground. Broad-leaved tree species including *D. sissoo* and *Eucalyptus camaldulensis* Dehnh. were observed 30–50 m away from the collection site.

The specimens were photographed at the sampling site, and the macroscopic characters were recorded in the field. Munsell (1975) was followed for color notation. The specimens were air dried for further analyses and deposited in the Herbarium of University of the Punjab, Quaid-e-Azam Campus, Lahore, Pakistan (LAH).

For microscopic studies, tissues from different parts of the basidiomata were rehydrated in KOH (2%) and mounted in Congo red (1%). Micro-morphological features were measured using calibrated Motic Images Plus 2.0 software. Genomic DNA was extracted using Extract-N-Amp™ kit following manufacturer's instructions. PCR amplification of the internal transcribed spacer region was carried out using ITS1F/ITS4 primer combination (White & al. 1990, Gardes & Bruns 1993). PCR products were purified and both strands were sequenced from Beijing Genomic Institute (BGI), P.R. China.

For phylogenetic analysis, consensus sequences were generated in BioEdit (Hall 1999) and BLAST searched at NCBI (https://www.ncbi.nlm.nih.gov/) to retrieve the sequences of closely related *Chlorophyllum* spp. from the database. Sequences mentioned in the published literature were also included from the database in final ITS matrix to represent different sections in the genus (Ge & al. 2018). *Agaricus campestris* L. was chosen as the outgroup. All the sequences were aligned online using MUSCLE (Edgar 2004). The final aligned data set was analyzed through MEGA 6.0 software for reassessing the phylogeny. Tamura 3-parameter (Tamura 1992) was selected as evolution model for maximum likelihood analysis using best-fit substitution model approach in MEGA (Tamura & al. 2013). A discrete gamma

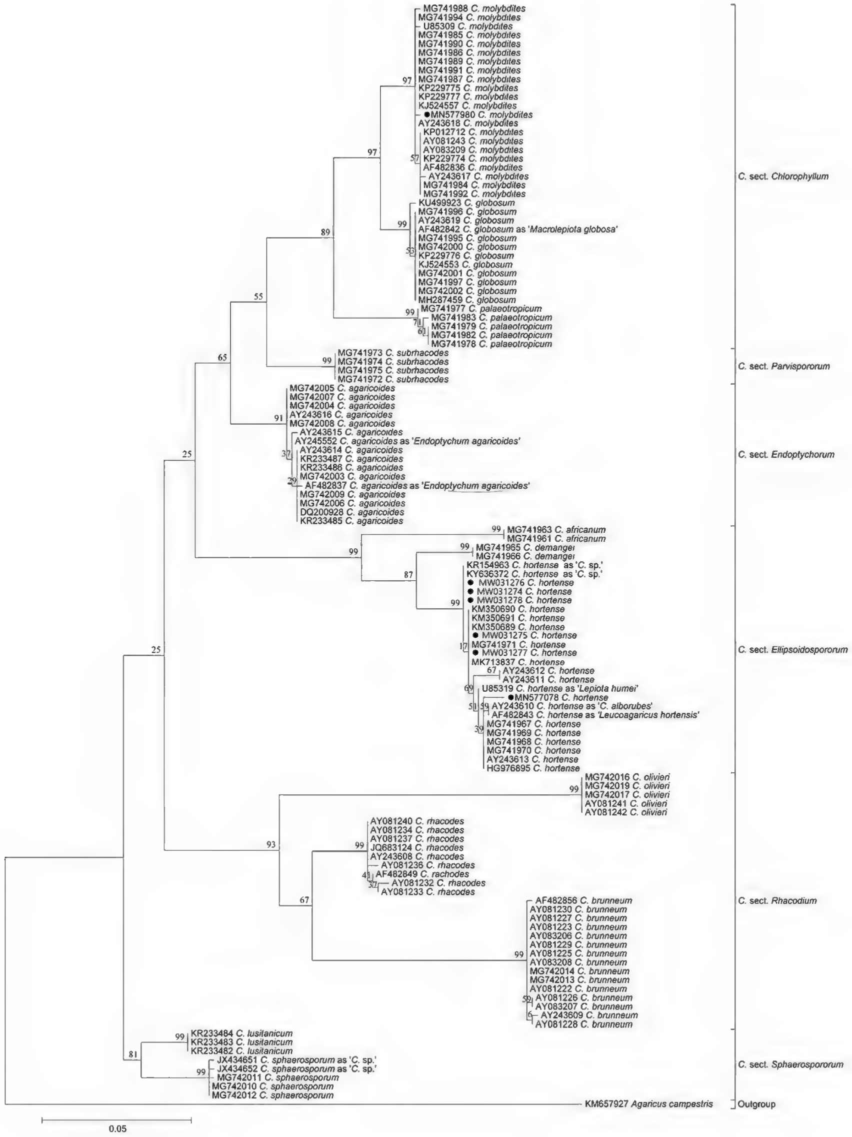

FIGURE. 1. Molecular phylogenetic analysis of ITS sequences of *Chlorophyllum* species. Section names are given on the right. The sequences generated during this study are marked with bullets.

distribution was used to model evolutionary rate differences among sites (5 categories (+G, parameter = 0.2606)).

Phylogenetic results

The ITS dataset included a total of 125 nucleotide sequences. There were a total of 726 positions in the final matrix. All positions were used in the analysis. Among these positions, 477 were conserved, 227 were variable, 183 were parsimony informative. The maximum likelihood tree is given in Figure 1. There were total six major clades representing six infrageneric groups and an outgroup. The topology of the tree is similar to the previous phylogeny reconstructed by Ge & al. (2018). The sequences from Pakistani collections clustered within *C.* sect. *Chlorophyllum* Massee (*C. molybdites*) and *C.* sect. *Ellipsoidospororum* Z.W. Ge (*C. hortense*) along with similar sequences of *Chlorophyllum* species from different parts of the world.

Taxonomy

Chlorophyllum hortense (Murrill) Vellinga, Mycotaxon 83: 416 (2002) Figs 2a–d, 3

Basidiomata agaricoid. Pileus 3–6.1 cm broad, slightly umbonate, conical to convex and flat at maturity; central disc yellowish brown (7.5YR5/8); surface dry, matt, scaly, scales furfuraceous, radially arranged, concentrated near the center and sparse towards margins; squamules present towards the margins, grayish (10Y7/2); margin slightly striate and cracked or wavy. Lamellae crowded, free, off-white (2.5Y9/2) to yellowish green (10Y9/4), with entire white edge. Lamellulae lengths variable. Stipe 9.1 × 1 cm, cylindrical; base slightly broadening ≤1.4 cm; surface longitudinally striate; striations light yellowish brown (2.5Y7/4), slightly pink (10P7/10) at the site of attachment with the pileus and around the annulus. Annulus double, superior, persistent, having pinkish tint close to the stipe. Context soft, brittle, white, becoming pinkish (10P7/10) when bruised.

Basidiospores [70/6/6] (6.8–)7.2–9.4(–10.8) × (5.3–)5.8–6.4(–6.8) µm, Q = (1.2–)1.3–1.4(–1.5), avQ = 1.3, ellipsoid with rounded apex, thick walled; germ pore absent; dextrinoid, reddish in Congo red. Basidia (24–)24.8–31.2(–34.9) × (8.7–)9–10.3(–11.8) µm, clavate, 2–4 sterigmata, most commonly 2-sterigmate. Lamellae edge sterile. Cheilocystidia (28.6–)35.2–58.9(–62.1) × (6.2–)7.3–9(–9.9) µm subcylindric to slightly fusiform or very narrowly clavate. Pleurocystidia absent. Pileipellis hyphae (from the background) (4.2–)6.2–9.1(–10) µm in diameter, long, cylindrical, frequently septate, branched; terminal elements clavate to narrowly clavate

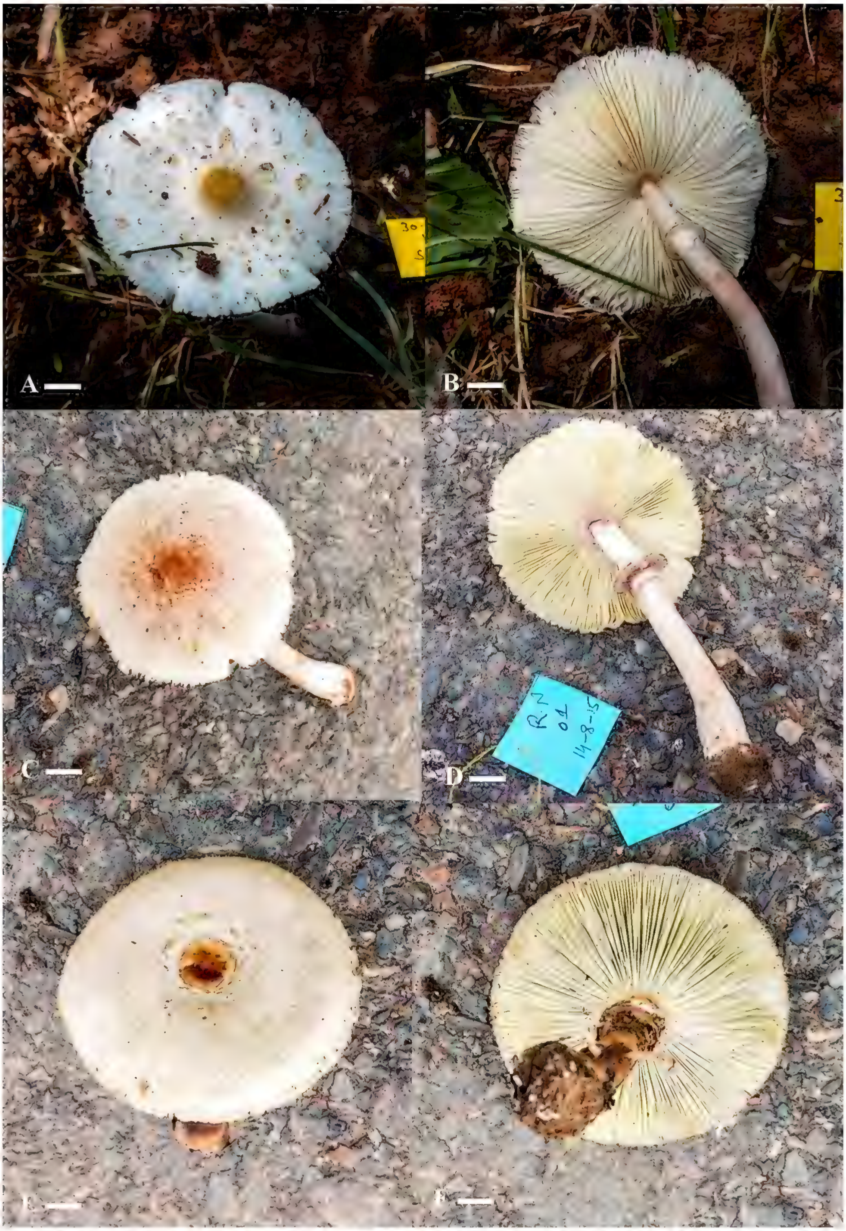

FIGURE. 2. ***Chlorophyllum hortense*** basidiomata: A, B. LAH36664; C, D. LAH36661. ***Chlorophyllum molybdites*** basidioma: E, F. LAH36660. Scale bars = 1 cm. Photographs by Mughees Hamid and Humaira Bashir.

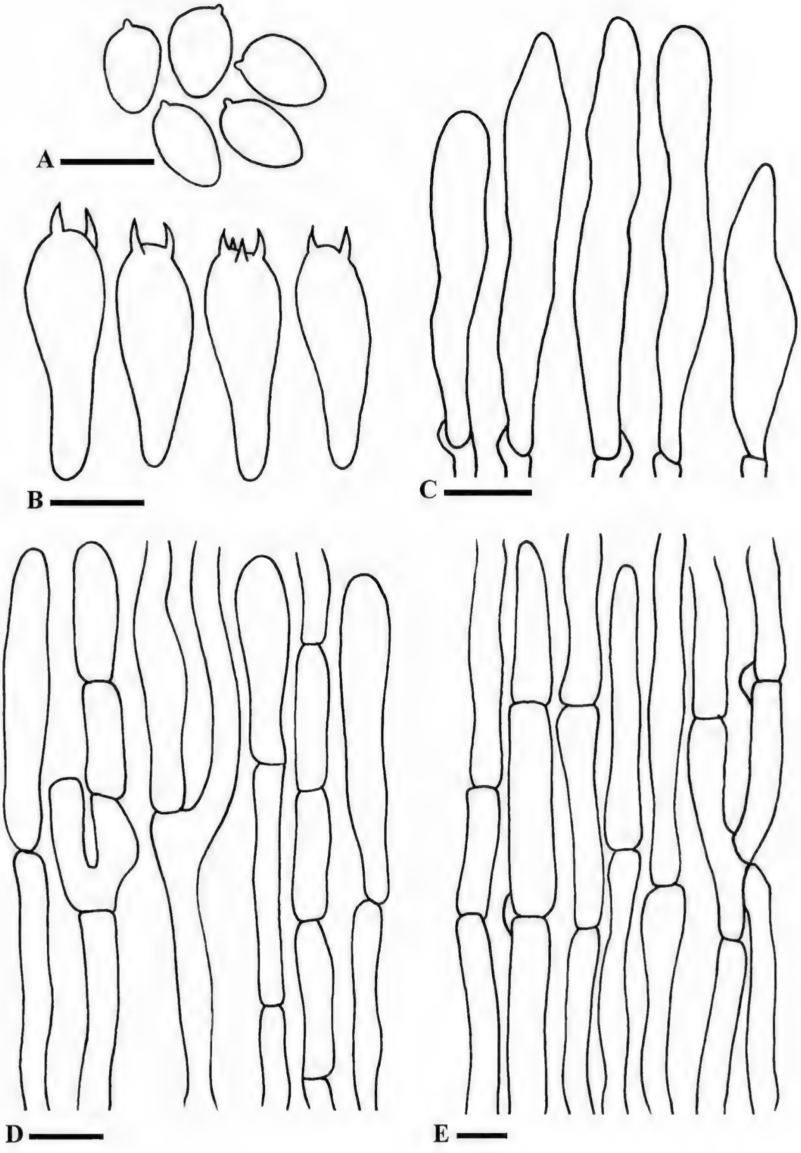

Figure. 3. *Chlorophyllum hortense* [LAH36661]. A. Basidiospores; B. Basidia; C. Cheilocystidia; D. Pileipellis (hyphae from the background); E. Stipitipellis. Scale bars = 10 µm. Drawing by Sana Jabeen.

forming a trichoderm, pale yellow from the disc and hyaline from the margins in KOH. STIPITIPELLIS hyphae (7.2–)8.2–10.2(–10.4) µm wide, filamentous, branched, with narrow terminal cells, septate, clamped septa rare, hyaline in KOH.

MATERIAL EXAMINED: **PAKISTAN. PUNJAB, Gujranwala division**, Narowal district, Bola Bajwa, 234 m asl, on soil, 14 August 2015, Humaira Bashir RN1S53 (LAH36661; GenBank MN577078); **Lahore division**, Kasur district, near BRB Canal, 218 m asl, on soil, 30 July 2019, Mughees Hamid S#3SJ45 (LAH36662; GenBank MW031274); S#7SJ37 (LAH36663; GenBank MW031275); S#6SJ44 (LAH36664; GenBank MW031276); 1 August 2019 Mughees Hamid S#28SJ38 (LAH36665; GenBank MW031277); 9 August 2019 Mughees Hamid S#63SJ42 (LAH36666; GenBank MW031278).

Chlorophyllum molybdites (G. Mey.) Massee,
Bull. Misc. Inf., Kew 1898(138): 136 (1898) FIGS 2 E,F, 4

BASIDIOMA agaricoid. PILEUS 7.6 cm in diameter, spherical when young, plane when mature; margins slightly cracked; central disc plate-like, brownish black (7.5YR3/6) to dull yellow orange (10YR6/10); surface creamy white (5Y9/4), minutely pubescent with distinct brown fibrils and patches of squamules; squamules uplifted, dull yellow orange (10YR6/10), concentrated near the center. LAMELLAE free, crowded, regular, even, light green (5GY8/4), edges entire. LAMELLULAE three tiered. STIPE 6.3 × 0.8 cm, cylindrical, straight to bent, slightly bulbous at the base, light brown (10YR5/6) to dark brown (10YR3/6), central to the pileus; surface smooth, dry, glabrous. ANNULUS double edged, edges ruptured, persistent, fixed, central to the stipe, upper surface white, lower surface brown. CONTEXT slightly tough, and hard particularly of stipe, white, becoming pinkish (10P7/10) when bruised.

BASIDIOSPORES [20/1/1] (8.6–)9.3–12.2(–12.5) × (6–)6.6–7.7(–7.8) µm, Q = (1.2–)1.3–1.5(–1.6), avQ = 1.3, ellipsoid to amygdaliform, smooth, with truncate apex and visible germ pore and prominent apiculus, thick-walled, dextrinoid, pinkish in Congo red, light green in 5% KOH. BASIDIA (22.8–)24–28.6(–29.6) × (10.1–)10.6–13.5(–14) µm, clavate, 2–4 sterigmate, thin-walled. LAMELLA EDGE sterile. CHEILOCYSTIDIA (20–)24.3–28.8(–31.1) × (7.6–)8.3–10.2(–11.7) µm, clavate to broadly clavate or sphaeropedunculate, hyaline to yellowish in KOH. PLEUROCYSTIDIA absent. PILEIPELLIS (hyphae from the background) trichoderm, hyphae forming a palisade of cells (7.6–)10.1–14(–14.7) µm in diameter, apical cells narrowly clavate and slightly long, pale yellow to brownish from the central disc and hyaline from the margins in 5% KOH. STIPITIPELLIS hyphae (3.5–)4.9–8.3(–8.8) µm wide, filamentous, branched, frequently septate, clamped septa rare, broad terminals, hyaline in KOH.

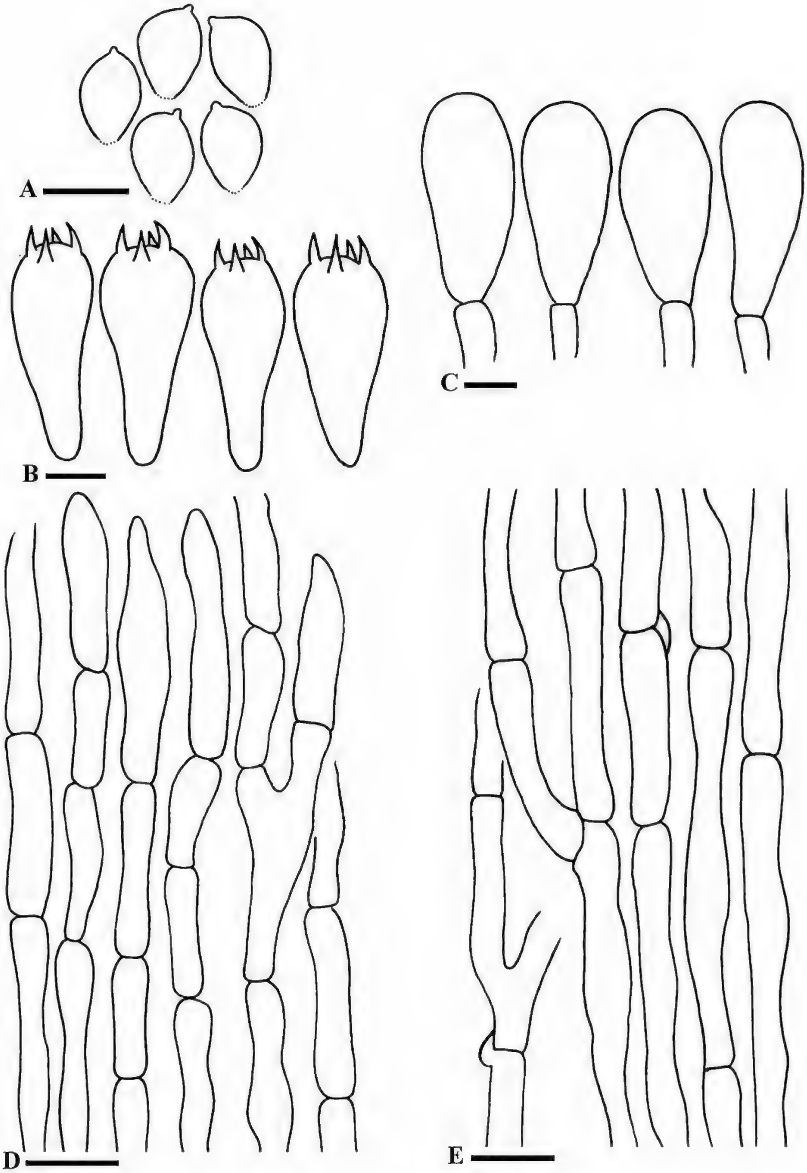

Figure. 4. *Chlorophyllum molybdites* [LAH36660]. A. Basidiospores; B. Basidia; C. Cheilocystidia; D. Pileipellis (hyphae from the background); E. Stipitipellis. Scale bars: A–C = 10 µm; D, E = 20 µm. Drawing by Sana Jabeen.

Material examined: **PAKISTAN. Punjab, Gujranwala division**, Narowal district, Bola Bajwa, 234 m asl, on soil, 14 August 2015, Humaira Bashir RN2 (LAH36660; GenBank MN577080).

Discussion

Two *Chlorophyllum* species from Kasur and Narowal district, Punjab, Pakistan have been identified. Both species have brown scales on the cap, which differ slightly in shape, but the main differences are in the color of the lamellae, spores, basidia, and cheilocystidia.

Chlorophyllum hortense was previously known under different species names in multiple genera including *Lepiota* (Pers.) Gray, *Leucoagaricus* Locq. ex Singer, and *Macrolepiota* Singer, until Vellinga (2003a) used molecular data and placed the taxon in *Chlorophyllum*. It is placed in *C.* sect. *Ellipsoidospororum,* characterized by slender basidiomata having furfuraceous squamules on the pileus, ellipsoid basidiospores without a germ pore, and subcylindric to slightly fusiform cheilocystidia (Ge & al. 2018). This species can be separated from other taxa in *C.* sect. *Ellipsoidospororum* by its white basidiomata, ellipsoid basidiospores with a rounded apex and lack of a germ pore, frequent 2-spored basidia, and subcylindric to fusiform cheilocystidia (Ge & al. 2018). It should be noted that although 2-spored basidia are rare in the *Agaricaceae,* we have frequently observed 2-spored basidia both previously and during this investigation. These specimens showed remarkable similarity with previous descriptions of the species by several workers from different parts of the world (Murrill 1914, Pegler 1983, Aberdeen 1992, Akers & Sundberg 1997, Vellinga 2003a, Ge & Yang 2006, Nascimento & Alves 2014, Alves & al. 2016). Clamp connections were also observed in the stipitipellis of Pakistani collections. Distinct clamp connections were reported by Akers & Sundberg (1997) and Vellinga (2003a), but not observed by Pegler (1983) and Ge & Yang (2006).

Chlorophyllum hortense is widely distributed and known (under various names) from Africa, Asia, Australia, and North and South America (Murrill 1914, Dennis 1952, Aberdeen 1962, 1992; Smith 1966; Heinemann 1973; Pegler 1983, 1997; Franco 1994; Akers & Sundberg 1997; Vrinda & al. 1999; Hemmes & Desjardin 2002; Vellinga 2003a; Sobestiansky 2005; Ge & Yang 2006; Gimenes 2007; Farook & al. 2013; Nascimento & Alves 2014; Alves & al. 2016).

Chlorophyllum molybdites [= *C. esculentum* Massee, the generic type] is characterized by olive to greenish-white basidiospores with a truncate apex, broadly clavate to sphaeropedunculate cheilocystidia, and a palisade-like pileus covering of hyphae with terminal clavate to subfusiform elements (Ge & al. 2018). The specimen identified as *C. molybdites* during this investigation showed similar characters as described by Pegler (1983), De Meijer & al. (2007), Alves & al. (2016, 2019), and Bijeesh & al. (2017). It is characterized by the green lamellae and green basidiospores (>10 µm) with a truncate apex and a prominent germ pore (Ge & al. 2018, Alves & al. 2019). This species is considered toxic and causes gastrointestinal distress; the symptoms can be quite serious. The toxicity of this species may depend upon climatic conditions, habitat alone, and the susceptibility of the individual (Graff 1927, Pegler 1983, Reid & Eicker 1991, Lehmann & Khazan 1992; Benjamin 1995). This species has been reported worldwide (Reid & Eicker 1991).

Chlorophyllum molybdites has been reported previously in the cold desert climate of Gilgit-Baltistan, Pakistan (Razaq & Shahzad 2012). Photographs by Razaq & Shahzad (2012) show a specimen with persistent scales that are grayish rather than dark brown and the lamellae appear white, which also differs from previous descriptions of *C. molybdites*. Since Razaq & Shahzad's (2012) identification was based solely on macroscopic characters without detailed anatomical observations and lacking a herbarium specimen and phylogenetic analyses, their Pakistan report of *C. molybdites* cannot be authenticated.

Chlorophyllum rhacodes (Vittad.) Vellinga [≡ *Macrolepiota rhacodes* (Vittad.) Singer] has also been reported from Pakistan (Razaq & Shahzad 2012, as *Macrolepiota*). *Chlorophyllum rhacodes* can be identified by large basidiomata with darker pileus scales and a bulbous stipe with a double crowned annulus. Anatomically this species can be distinguished from other *Chlorophyllum* species by its large, broad (10–35 × 8.5–25 µm) sphaeropedunculate cheilocystidia. Its basidiospores are 8.8–12.7 × 5.4–7.9 µm with a rounded to truncate apex and visible germ pore, and its pileipellis is a tightly packed hymeniderm of cylindrical and flexuous, or narrowly clavate or narrowly lageniform elements (Vellinga 2003b). The Pakistani collection identified as *Macrolepiota rhacodes* by Razaq & Shahzad (2012) shared some features with the type specimen, including the larger basidiomata with dark brown scales, double crowned annulus, a stipe with bulbous base; and the spore shape and size (Razaq & Shahzad 2012). We can conclude that *M. rhacodes* described by Razaq & Shahzad (2012) probably represents *C. rhacodes*; but again, without an herbarium specimen, we cannot obtain the detailed description and molecular phylogeny necessary to authenticate this record.

This investigation reports *C. hortense* as a new record from Pakistan and confirms the occurrence of *C. molybdites* from Pakistan, based on detailed morphological descriptions and molecular phylogenetic evidence. Occurrence of *Chlorophyllum* species in Pakistan considerably extends their known distribution into warm semi-arid and humid subtropical regions.

Acknowledgements

Sincere thanks to Dr. Else C. Vellinga (University of California, Berkeley, California, USA) and Dr. Chang-Lin Zhao (Southwest Forestry University, Kunming, Yunnan, P.R. China) for presubmission review of the manuscript. Their comments and suggestions greatly helped to improve the document.

Literature cited

Aberdeen JEC. 1962. Notes on Australian *Lepiota* in the Kew Herbarium. Kew Bulletin 16: 129–137. https://doi.org/10.2307/4120357

Aberdeen JEC. 1992. Lepiotoid genera (*Agaricales*) in south-eastern Queensland. Aberdeen Publications, Gailes, Queensland.

Akers BP, Sundberg WJ. 1997. *Leucoagaricus hortensis*: some synonyms from Florida and taxonomic observations. Mycotaxon 62: 401–419.

Alves RP, Menezes GCA, Oliveira ED, Victoria FC, Pereira AB, Albuquerque MP. 2016. *Chlorophyllum* Massee e *Macrolepiota* Singer (*Agaricaceae*) em área do bioma Pampa, Rio Grande do Sul, Brasil. Neotropical Biology and Conservation 11(3): 141–152. https://doi. org/10.4013/nbc.2016.113.04

Alves MH, Cruz MO, Nascimento CC. 2019. First record of *Chlorophyllum molybdites* (G. Mey.) Massee (*Basidiomycota*, *Agaricaceae*) from Piauí state, Brazil. Check List 15(5): 695–699. https://doi.org/10.15560/15.4.695

Benjamin DR. 1995. Mushrooms, poisons and panaceas: a handbook for naturalists, mycologists and physicians. Freemann WH and Co., New York. 422 p.

Bijeesh C, Vrinda KB, Pradeep CK. 2017. Mushroom poisoning by *Chlorophyllum molybdites* in Kerala. Journal of Mycopathological Research 54 (4): 477–483.

Crous PW, Wingfield MJ, Guarro J, Hernandez-Restrepo M, Sutton DA, Acharya K & al. 2015. Fungal planet description sheets: 320–370. Persoonia 34: 167–266. https://doi.org/10.3767/003158515x688433

De Meijer AAR, Amazonas MALA, Rubio GBG, Curial RM. 2007. Incidences of poisonings due to *Chlorophyllum molybdites* in the state of Paraná, Brazil. Brazilian Archives of Biology and Technology 50(3): 479–488. https://doi.org/10.1590/S1516-89132007000300014

Dennis RWG. 1952. *Lepiota* and allied genera in Trinidad, British West Indies. Kew Bulletin. 7(4): 459–499. https://doi.org/10.2307/4117800

Edgar RC. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research 32(5): 1792–1797. https://doi.org/10.1093/nar/gkh340

Farook VA, Khan SS, Manimohan P. 2013. A checklist of agarics (gilled mushrooms) of Kerala State, India. Mycosphere 4(1): 97–131. https://doi.org/10.5943/mycosphere/4/1/6

Franco AE. 1994. The genus *Lepiota* sensu stricto with observations on related taxa in Colombia. Ph.D. Dissertation. City University of New York.

Gardes M, Bruns TD. 1993. ITS primers with enhanced specificity of basidiomycetes: application to the identification of mycorrhizae and rusts. Molecular Ecology 2: 113–118. https://doi.org/10.1111/j.1365-294X.1993.tb00005.x

Ge ZW, Yang ZL. 2006. The genus *Chlorophyllum* (*Basidiomycetes*) in China. Mycotaxon 96: 181–191.

Ge ZW, Jacobs A, Vellinga EC, Sysouphanthong P, Walt R, Lavorato C, Yang ZL. 2018. A multi-gene phylogeny of *Chlorophyllum* (*Agaricaceae*, *Basidiomycota*): new species, new combination and infrageneric classification. MycoKeys 32: 65–90. https://doi.org/10.3897/mycokeys.32.23831

Geiger R. 1954. Klassifikation der Klimate nach W. Köppen. Landolt-Börnstein – Zahlenwerte und Funktionen aus Physik, Chemie, Astronomie, Geophysik und Technik, alte Serie,. 3: 603–607.

Geiger R.. 1961. Überarbeitete Neuausgabe von Geiger, R.: Köppen-Geiger / Klima der Erde. (Wandkarte 1:16 Mill.). Klett-Perthes, Gotha.

Gimenes LJ. 2007. A tribo *Leucocoprineae (Agaricaceae)* no Parque Estadual das Fontes do Ipiranga, São Paulo, SP, Brasil. PhD thesis, Biodiversidade Vegetal e Meio Ambiente, Instituto de Botânica da Secretaria do Meio Ambiente, São Paulo.

Graff PW. 1927. The green-spored *Lepiota*. Mycologia 19: 322–326. https://doi.org/10.1080/00275514.1927.12020565

Hall TA. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acid Series 41: 95–98.

Heinemann P. 1973. Leucocoprinées nouvelles d'Afrique centrale. Bulletin du Jardin Botanique National de Belgique 43: 7–13. https://doi.org/10.2307/3667558

Hemmes DE, Desjardin DE. 2002. Mushrooms of Hawaii: an identification guide. Ten Speed Press. Berkeley, California. 212 p.

Lehmann PF, Khazan U. 1992. Mushroom poisoning by *Chlorophyllum molybdites* in the Midwest United States. Mycopathologia 118: 3–13. https://doi.org/10.1007/BF00472564

Loizides M, Alvarado P, Polemis E, Dimou DM, Zervakis GI, Thines M, Telle S, Konstantinou G, Gube M. 2020. Multiple evolutionary origins of secotioid species in the agaricoid genus *Chlorophyllum*. Mycologia 112: 400–422. https://doi.org/10.1080/00275514.2020.1712179

Munsell AH. 1975. Munsell Soil Color Charts. Macbeth Division of Kollmorgen Corporation. Baltimore, Maryland.

Murrill WA. 1914. *Agaricaceae*. North American Flora 10(1): 41–65.

Nascimento CC, Alves MH. 2014. New records of *Agaricaceae* (*Basidiomycota*, *Agaricales*) from Araripe National Forest, Ceará State, Brazil. Mycosphere 5(2): 319–332. https://doi.org/10.5943/mycosphere/5/2/6

Pegler DN. 1983. Agaric flora of the Lesser Antilles. Kew Bulletin Additional Series 9. 668 p.

Pegler DN. 1997. The agarics of São Paulo: an account of the agaricoid fungi (*Holobasidiomycetes*) of São Paulo State, Brazil. Royal Botanic Gardens, Kew. 68 p.

Razaq A, Shahzad S. 2012. New records of *Agaricaceae* form Pakistan. Pakistan Journal of Botany 44(4): 1475–1477.

Reid DA, Eicker A. 1991. A comprehensive account of *Chlorophyllum molybdites*. Botanical Bulletin Academia Sinica 32: 317–334.

Smith HV. 1966. Contributions toward a monograph on the genus *Lepiota*, I. Type studies in the genus *Lepiota*. Mycopathologia et Mycologia Applicata 29: 97–117. https://doi.org/10.1007/BF02055063

Sobestiansky G . 2005. Contribution to a macromycete survey of the states of Rio Grande do Sul and Santa Catarina in Brazil. Brazilian Archives of Biology and Technology 48(3): 437–457. https://doi.org/10.1590/S1516-89132005000300015

Tamura K. 1992. Estimation of the number of nucleotide substitutions when there are strong transition-transversion and G + C-content biases. Molecular Biology and Evolution 9: 678–687.

Tamura K, Stecher G, Peterson D, Filipski A, Kumar S. 2013. MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. Molecular Biology and Evolution 30: 2725–2729. https://doi.org/10.1093/molbev/mst197

Vellinga EC. 2003a. *Chlorophyllum* and *Macrolepiota* (*Agaricaceae*) in Australia. Australian Systematic Botany 16: 361–370. https://doi.org/10.1071/sb02013

Vellinga EC. 2003b. Type studies in *Agaricaceae—Chlorophyllum rachodes* and allies. Mycotaxon 85: 259–270.

Vellinga EC. 2004a. Ecology and distribution of lepiotaceous fungi (*Agaricaceae*) - A review. Nova Hedwigia 78: 273–299. https://doi.org/10.1127/0029-5035/2004/0078-0273

Vellinga EC. 2004b. Genera in the family *Agaricaceae*: evidence from nrITS and nrLSU sequences. Mycological Research 108: 354–377. https://doi.org/10.1017/s0953756204009700

Vellinga EC, Sysouphanthong P, Hyde KD. 2011. The family *Agaricaceae*: phylogenies and two new white-spored genera. Mycologia 103: 494–509. https://doi.org/10.3852/10-204

Vrinda KB, Pradeep CK, Mathew S. Abraham TK. 1999. *Agaricales* from Western Ghats–VII. Mushroom Research 8(2): 9–12.

White TJ, Bruns T, Lee S, Taylor J. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. 315–322, in: MA Innis & al. (eds). PCR protocols: a guide to methods and applications. Academic Press, San Diego. https://doi.org/10.1016/B978-0-12-372180-8.50042-1